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Living to fight another day: The ecological and evolutionary significance of Neanderthal healthcare

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ABSTRACT

Evidence of care for the ill and injured amongst Neanderthals, inferred through skeletal evidence for survival from severe illness and injury, is widely accepted. However, healthcare practices have been viewed primarily as an example of complex cultural behaviour, often discussed alongside symbolism or mortuary practices. Here we argue that care for the ill and injured is likely to have a long evolutionary history and to have been highly effective in improving health and reducing mortality risks. Healthcare provisioning can thus be understood alongside other collaborative 'risk pooling' strategies such as collaborative hunting, food sharing and collaborative parenting. For Neanderthals in particular the selective advantages of healthcare provisioning would have been elevated by a variety of ecological conditions which increased the risk of injury as well their particular behavioural adaptations which affected the benefits of promoting survival from injury and illness. We argue that healthcare provisioning was not only a more significant evolutionary adaptation than has previously been acknowledged, but moreover may also have been essential to Neanderthal occupation at the limits of the North Temperate Zone.

1. Introduction

Cases of apparent care for Neanderthals who were injured or suffered severe illnesses have been seen as evidence for complex cultural behaviour in these archaic hominins. However the potential evolutionary significance of Neanderthal healthcare is often overlooked.

Here we review evidence for recovery from serious illness and injury and conclude that Neanderthal healthcare was widespread, knowledgeable and effective in reducing mortality risk. We argue that healthcare, from likely short term treatment for minor injuries and illnesses as well as long term and significant accommodations, functions to reduce the risks posed by injury and illness. We situate Neanderthal healthcare within an evolutionary history of care for the ill and injured as an adaptive practice, and consider how the particular ecological challenges faced by Neanderthals may explain pressures to reduce mortality risk from injury through healthcare.

We argue that rather than simply a cultural trait, healthcare can be seen as part of several adaptations which allowed Neanderthals to survive in unique environments where they lived alongside large predatory carnivores and were often dependant on large mammal biomass as a major food source. Moreover healthcare it may have been a significant factor in allowing Neanderthals to occupy a predatory niche which might otherwise have been unavailable to them.

1.1. Neanderthal healthcare as enigmatic cultural practice

Evidence for remarkable survival of Neanderthals who were ill or injured has been recovered since as far back as the mid nineteenth century. The limited remains of one of the earliest Neanderthals discovered, the Feldhofer Neanderthal or 'Neanderthal 1' individual, discovered in 1856, demonstrated recovery with likely care from several injuries and illnesses for example. These included a severe fracture of the left arm and a healed injury to the frontal bone as well as continued survival with extensive inflammation of the paranasal sinuses and metastatic disease (Schultz, 2006). Care over his lifetime may have included short term intensive care when

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injured, accommodation for a lack of movement in the arm in foraging for food, as well as probable care for systemic disease prior to death. He was not alone with many other Neanderthals displaying a range of severe injuries and pathologies before death. Injuries appear to have been common in these archaic hominins, and most Neanderthals appear to have suffered from some traumatic injury and recovery, often several cases of such (Berger and Trinkaus, 1995; Trinkaus, 2012). That Neanderthals were capable of caring for individuals who were ill or injured, from the provisioning of food, water and protection to active treatment for injuries, is widely accepted (Hublin, 2009; Thorpe, 2016; Trinkaus and Villotte, 2017).

Healthcare has however typically been regarded as a complex cultural practice without an obvious adaptive function. This is at least in part due to most attention being paid to cases where care needs must have been extensive, requiring high levels of daily input over long time scales. Such cases are 'costly' in evolutionary terms as great efforts are made to help someone survive who apparently could give little back in return, and are seen as good evidence that the motivations for care from others were 'uncalculating' (Spikins et al., 2018). Perhaps the most famous individual benefitting from such care, Shanidar I, survived for at least a decade despite a withered arm, damaged leg, probable blindness in one eye and probable hearing loss through what is likely to have been daily care and provisioning from others (Crubézy and Trinkaus, 1992; Trinkaus and Zimmerman, 1982; Trinkaus, 2014; Trinkaus and Villotte, 2017). Trinkaus and Shipman comment that *'A one-armed, partially blind, crippled man could have made no pretense of hunting or gathering his own food. That he survived for years after his trauma was a testament to Neandertal compassion and humanity' (*Trinkaus and Shipman, 1993, 341). Extended periods of interpersonal care, despite a lack of any overall economic benefit to such care, is also clearly evident in other cases such as that of La Chapelle aux Saints I who suffered from several debilitating conditions, including severe osteoarthritis and systemic disease (Tilley, 2015a). Tilley comments *'it seems unquestionable that during the last months of LC1's life, at least, the effects of these pathologies, both individually and in combination, would have constituted loss of independence — and therefore significant disability — when assessed within the Neanderthal lifeways context. The extent and impact of his pathologies suggest that LC1 needed and received health-related care provision to achieve survival to age at death*' (Tilley, 2015a, 235). Most older Neanderthals have healed pathologies prompting Trinkaus and Zimmerman to comment *'that the Neanderthals had achieved a level of societal development in which disabled individuals were well cared for by others of the social group. … Several of them, particularly Shanidar 1 and 3, lived for many years with severely disabling conditions, which would have prevented them from actively contributing to the subsistence of the local group'* (Trinkaus and Zimmerman, 1982, 75).

Given the apparently costly nature of healthcare it is unsurprising that care is typically discussed as a somewhat enigmatic cultural practice, alongside mortuary practices and symbolism.

The significance of healthcare as part of Neanderthal *adaptation* remains to be fully explored.

1.2. A broader pattern of widespread cases of recovery, survival and care

Cases of recovery from severe injury or illness are often discussed in isolation. However despite a limited skeletal sample a closer consideration of the pattern of evidence for probable care reveals many cases in which recovery or survival from pathology and trauma indicate likely highly effective care from others (Table 1), distributed throughout the period and spatial extent of Neanderthal occupation (Fig. 1).

There have been debates over the precise levels of care implied by recovery in particular cases (for discussion (see Spikins et al., 2018) however recovery from severe illness or injury aided by care seems relatively common. As well as other cases, fractures to the main weight bearing bones of La Ferrassie 1, and La Ferrassie 2 are likely to have entailed care from others to ensure recovery, whilst a break or sprain of the left foot of Shanidar 3 is also likely to have entailed support as would the recovery from serious cranial injuries seen in St Cesaire 1 and Krapina 37. In several cases healthcare or support is likely to have been long term, with severe periodontal inflammation likely to have restricted the capacity of Aubesier 11 and Guattari 1 to forage for themselves, and serious arm injuries likely to also make foraging (and certainly hunting activities) difficult for the Feldhofer Neanderthal (Neanderthal 1), Krapina 180 and La Quina 5 (for further details of these cases see (Trinkaus and Zimmerman, 1982; Fennell and Trinkaus, 1997; Zollikofer et al., 2002; Trinkaus et al., 2008a, 2008b; Hublin, 2009; Estabrook, 2009; Thorpe, 2016; Tilley, 2015a; Cunha, 2016; Trinkaus and Villotte, 2017).

Healthcare also seems likely to have been knowledgeable and remarkably *technical*ly *competent* in Neanderthals. In the case of La Chapelle aux Saints 1, for example, care when most debilitated is likely to have included fever management, hygiene maintenance and repositioning and manipulation (Tilley, 2015a). Individuals with systemic diseases (such as La Chapelle aux Saints 1) would have needed to have been kept hydrated to manage fever, whilst those with severe wounds and fractures would have required adequate nutrition and rest. A femoral fracture at the greater trochanter of La Ferrassie 1 for example would have been painful and severely restricted mobility requiring care and provisioning (Fennell and Trinkaus, 1997), as would chronic osteomyelitis of the hip in La Chapelle aux Saints 1 (Tilley, 2015a). High rates and healing and low rates of infection suggest that some form of wound management may have been common (Trinkaus and Zimmerman, 1982, 75). This may have involved using particular dressings and means of reducing blood loss. The Inuit for example killed lemmings to use their skins for dressings wounds and boils, but only rarely ate lemming meat (Mcelroy et al., 2009, 19). Ochre may potentially have been used as an antiseptic when applied to wounds (Zilhão et al., 2010; Velo, 1984). There is also evidence for use of the use of medicinal plants in dental calculus (Hardy et al., 2012; Hardy, 2018), including poplar, which contains salicylic acid and may have been used as a painkiller (Weyrich et al., 2017).

Neanderthals appear to also have been expert collaborative healthcare providers. Moreover, the visible archaeological evidence is likely to be the 'tip of the iceberg' of more common healthcare practices, the majority of which remain invisible to archaeological interpretation.

1.3. Healthcare and differential archaeological visibility

The most archaeologically visible cases of healthcare tend to be particularly 'costly' (in terms of efforts invested from others with little apparent return) thus skewing our understanding of the adaptive role of caring for the ill and injured. However what is visible in the anatomical record poorly represents likely typical healthcare practices. A well known 'osteological paradox' affects how we make interpretations of health, disease and care from skeletal material (Bishop, 2011). The skeletal record is biased as to which individuals are preserved, only certain elements may be present, and many diseases leave no evidence in bone. However these biases also specifically act to reduce the apparent adaptive value of healthcare practices in several ways. Only the most severe cases of pathology (such as bone trauma and severe degenerative

Table 1
Examples of recovery from pathology suggesting probable care in Neanderthal skeletal material.

site and date	specimen	age and sex	pathology	impact	care	references
Bau de l'Aubesier, France, c. 180,000 BP	Aubesier 11	Adult, female (?)	1. Extensive antemortem tooth loss 2. Broken teeth 3. Abscesses 4. Mandibular torus and torus lateralis superior	1–4 Pain, compromised mastication and incapacity to use teeth and tools, and with increased risk of infection due to broken teeth	1–4 Compromised masticatory apparatus may have required accommodation, both in helping with eating and with allowing other tasks to avoid using teeth as tools	(Lebel and Trinkaus, 2002)
Šal'a 1, Slovak Republic, c. OIS 5E	Šal'a 1	Prime aged adult, female	traumatic lesion to right supraorbital torus, with evidence of healing	Short term pain and possible cognitive disruption, long term possibly asymptomatic	given its location, short term care in cleaning the wound is likely	(Sladek, 2002; Wu et al., 2011a,2011b)
Regourdou, Montignac-sur-Vézère, France, MIS 5	Regourdou 1	Mid 20s, sex unknown	1. Osteoarthrosis of the spine with osteophytosis 2. abnormal bone growth to C4, 3. T2 ligamentum flavum ossification 4. T9 twisting of spinous process 5. L5 ossification of vertebral ligament insertion 6. fusion and asymmetry in the sacrum (possible scoliosis) 7. pathology in the femur, possibly linked to 6.	1–7 Pain and probable limitation to the range of movement available	1–7 Possible accommodation in the range of activities carried out	(Gómez-Olivencia et al., 2012, 2013; Maureille et al., 2015)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120–130,000 BP	Krapina 4	Not specified	Blunt force injury marked by an oval depression to the frontal bone, with evidence of healing and a purulent infection	Short term pain and blood loss and possible cognitive disruption, long term possibly asymptomatic	given its location, short term care in cleaning the wound is possible, though perhaps less likely than in other cases given the presence of infection	(Estabrook and Frayer, 2014)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120–130,000 BP	Krapina 5	Not specified	1. small blunt force traumas to the skull 2. periosteal reaction across the skull	1. possible short term pain and blood loss and possible cognitive disruption, long term possibly asymptomatic 2. possible pain or asymptomatic	1. given the location, cleaning the wound is possible 2. intervention unlikely	(Estabrook and Frayer, 2014)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120–130,000 BP	Krapina 20	Not specified	1. Two blunt force traumas to the frontal bone (possibly occurring at the same time), with no evidence of infection 2. diffuse periostitis, likely caused by a subcutaneous infection	1. possible short term pain and blood loss and possible cognitive disruption, long term possibly asymptomatic 2. possible pain or asymptomatic	1. given the location, cleaning the wound is possible 2. intervention unlikely	(Estabrook and Frayer, 2014)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120–130,000 BP	Krapina 31	adult	1. Depression to the frontal bone with evidence of healing 2. mild periostitis	1. possible short term pain and blood loss and possible cognitive disruption, long term possibly asymptomatic 2. possible pain or asymptomatic	1. given the location, cleaning the wound is possible 2. intervention unlikely	(Estabrook and Frayer, 2014)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120–130,000 BP	Krapina 34.7	adult	Significant posterior parietal depressed fracture, with some evidence of inflammation of the wound	Pain, blood loss, increased risk of infection and possible short and long term cognitive disturbance	the location of the wound suggests help in dressing and cleaning the wound may have been required over a short term period. If serious cognitive impairments resulted from the injury more substantial long term accommodation may have been required	(Kricun et al., 1999; Wu et al., 2011a,2011b; Estabrook and Frayer, 2014; Monge et al., 2013)
Krapina rockshelter, Hušnjakovo	Krapina 106-110	adult	High degree of degeneration to C4-C7, likely caused by trauma	Initial trauma would cause pain and possibly limit the range of mobility and function in the	Possibly accommodation and support in treating the initial trauma. The later degeneration	(Gardner and Smith, 2006)

(continued on next page)

Table 1 (*continued*)

site and date	specimen	age and sex	pathology	impact	care	references
Hill, northern Zagreb, Croatia, 120–130,000 BP				affected area. Possibly caused pain and if advanced may have been more severe and impacted upon nerve function	may not have required support or accommodation, unless the nerves were affected, in which instance the level of care might have been high and long term	
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120–130,000 BP	Krapina 120.71	Not specified	Fragment of rib with empty medullary chamber. An osteolytic lesion is present in the posterio-medial aspect of the shaft, corresponding with fibrous dysplasia	Fibrous dysplastic neoplasm can be asymptomatic or it can present with debilitating symptoms. Not possible to differentiate one from the other from the bones alone	If asymptomatic, no care or accommodation would be needed. If symptomatic, care and accommodation may have been significant and long term	(Monge et al., 2013)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120–130,000 BP	Krapina 149	Not specified	Fracture to the right clavicle, well healed, with no evidence of long term disability	Pain and limited or painful motion to the right upper part of the body	Possible short term accommodation for a number of weeks	(Estabrook and Frayer, 2014)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120–130,000 BP	Krapina 180	adult	Right distal ulnar fracture and pseudoarthrosis or possible amputation of the limb, with perhaps the latter more likely. No signs of infection.	Pain and restricted movement and use of the affected limb. Amputation would significantly modify the range of activities that could be carried out, though evidence the limb was still actively used	Breaks would require intervention to set the bones and would compromise activities that involved the affected area for a number of weeks and possibly months. An amputated limb would permanently compromise the individual and group behavioural modification would be needed, perhaps including engagement with different tasks or help with tasks	(Radovčić et al., 1988; Wu et al., 2011a,2011b; Estabrook and Frayer, 2014)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120–130,000 BP	Krapina 188.8	adult	Fracture to the proximal end of the left ulna, with some bowing, and no evidence of infection	Pain and restricted movement and use of the affected limb in the short term	Intact radius would provide splinting for a fractured ulna (bowing of the bone suggesting poor alignment before healing). Pain would compromise activities that involved the affected area for a number of weeks.	(Estabrook and Frayer, 2014; Trinkaus and Villotte, 2017)
North Sea 51°40′ northern latitude, 3°20′ eastern longitude, c. OIS 5e	Zeeland Ridges	young adult, male	Lesion to the orbital roof with thick sclerotic margin, which lacks periosteal new bone formation but with evidence for osteoclastic action - likely an epidermoid cyst	Typically asymptomatic but can have significant impacts, including: visual problems, pain and swelling, headaches, dizziness, disequilibrium, intracranial hypertension, convulsions, extradural hematoma, focal neurological signs, seizure. Though rare, these cysts can become malignant.	If asymptomatic, no care or accommodation would be needed. If symptomatic, long term care and accommodation would be required.	(Hublin et al., 2009)
Kiik-Koba, Crimea, OIS 4 or OIS 5	Kiik-Koba 1	40–50 years, male	1. Intervertebral ossifications/ stiffening of the vertebral column 2. hypercementosis of a mandibular canine linked to extreme wear or possible periodontal disease 3. enthesopathy associated with the quadriceps femoris tendon 4. ossification of intertarsal connective tissue and bony spurs to the left sulcus tali and left intermediate medial cuneiform bone 5. enthesopathies to the triceps surae tendon	1. pain and reduced bending and spinal rotation likely, possibility of trapped nerves 2. pain 3. pain and possibly limited use of the affected area in the short term 4. possibly asymptomatic but can cause pain and limit movement 5. possibly asymptomatic but can cause pain and limit movement 6. pain and may limit movement 7. may be asymptomatic	Short term care and accommodation to help recovery from broken bones and possibly long term support and accommodation to compensate for pain and some limitation to range of movement in the limbs and trunk	(Trinkaus et al., 2008a)

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Table 1 (*continued*)

site and date	specimen	age and sex	pathology	impact	care	references
			insertions and left calcaneous 6. possible osteomyelitis to two distal phalanges 7. right distal hallucal phalanx shows a rounded bony growth with possible muscle hypertrophy 8. abnormality to the right fifth proximal phalanx, likely the result of a fracture to the diaphysis 9. The ossification of tendons may be linked to strain and possible old age and over-use or DISH	8. pain and may limit movement for a number of weeks 9. pain and possibly limited mobility		
Shanidar Cave, Iraq, top of layer D, c. 45–70,000 BP	Shanidar 1	35–50 years, male	1. atrophy and limb paralysis in the right arm caused by a nerve injury 2. right humerus fractured in two places, with signs of heavy callus formation and healing, as well as the bone healing at an abnormal angle 3. break to the right humerus from amputation of the limb or pseudoarthrosis 4. osteomyelitic lesion to the right clavicle, likely the result of a soft tissue injury, with evidence of healed infection 5. abnormalities in the right foot, including a healed fracture to the fifth metatarsal, and degenerative joint disease (DJD), making movement painful 6. DJD in multiple locations and with ossification of connective tissue, lined to trauma 7. hyperostotic disease, based on the presence of otherwise unexplained osteophytes 8. advanced DJD to the right knee 9. broadening of the right talus relative to the left and the left tibia shows significant curvature, likely compensating for trauma in the right leg and foot 10. the cranium shows a wound to the scalp, as well as a crushing injury to the lateral side of the left orbit, with evidence of full healing prior to death 11. auditory exostoses to the left meatus - grade III, and yet more advanced in the right meatus - grade III, with bridging across the porus	1–3 Each would have been painful in the short to medium term, ultimately leading to the probable amputation of the lower portion of the limb 4. short term pain 5–9 Mobility was likely compromised - being slow and painful - over a long time period 10. short term pain and blood loss, probable blindness in the left eye or compromised binocular vision, long term cognitive impairment possible to the cerebral motor cortex 11. possible deafness in this ear or compromised 3D acoustics	1–4 Breaks and crush injuries would require intervention to set the bones and would compromise activities that involved the affected area for a number of weeks and possibly months. An amputated limb would permanently compromise Shanidar 1 and likely required individual and group behavioural modification, perhaps including engagement with different tasks or help with tasks. 5–9 Long term compromised mobility may have resulted in behavioural modification by the group to compensate 10–11 Compromised sensory and possibly cognitive functions may have similarly necessitated individual and group behaviour modification to compensate	(Trinkaus and Zimmerman, 1982; Crubézy and Trinkaus, 1992; Tilley, 2015b; Trinkaus and Villotte, 2017; Kent, 2017)
Layer D, Shanidar Cave, Iraq, c. >45,000 BP	Shanidar 2	20–35 years, male	DJD along the vertebral column	Mobility was possibly compromised, likely being painful	Long term: compromised mobility may have resulted in accommodation by the group to compensate	(Trinkaus and Zimmerman, 1982)

(*continued on next page*)

Table 1 (*continued*)

site and date	specimen	age and sex	pathology	impact	care	references
Layer D, Shanidar Cave, Iraq, c. >45,000 BP	Shanidar 3	35–50 years, male	1. trauma to the left ninth rib caused by a penetrating wound that likely collapsed the lung 2. right talocrural and talocalcaneal articulations, with signs of healing, 3. extreme DJD to the right foot and bony spurs to the distal fibula and right talus, likely caused by a break or sprain	1. blood loss and pain for a number of weeks and restricted breathing and reduced exercise tolerance 2–3 pain and restricted mobility in the short term and probable pain and compromised mobility in the long term	1. Days to weeks of intense care for projectile injury 2. long term accommodation for limited mobility	(Trinkaus and Zimmerman, 1982; Churchill et al., 2009a)
Layer D, Shanidar Cave, Iraq, c. >45,000 BP	Shanidar 4	35–50 years, male	1. minor DJD to the arms, hands and vertebral column 2. healed fracture of the seventh/eighth rib, evidenced by areas of callus, occurring shortly before the time of death 3. possible hyperostotic disease	1. likely asymptomatic 2. pain and some restriction to breathing, movement and physical tasks for a number of weeks 3. likely asymptomatic	2. probable accommodation for a number of weeks	(Trinkaus and Zimmerman, 1982; Crubézy and Trinkaus, 1992)
Layer D, Shanidar Cave, Iraq, c. >45,000 BP	Shanidar 5	35–50 years, male	1. scalp wound to the frontal bone with evidence of healing 2. Paramedial endocranial hyperostosis (enplaque type, grade I)	1. blood loss and pain 2. probably asymptomatic	1. the location of the wound suggests help in dressing and cleaning the wound may have been required over a short term period	(Trinkaus and Zimmerman, 1982; Wu et al., 2011a,2011b)
La Quina, Charente, France, 65,000 BP	La Quina 5	adult	1. hypoplasia/atrophy of the left humerus 2. Broken teeth	1. affected limb may have been restricted in its range of uses 2. increased likelihood of infection and loss of teeth, possible limitations in using teeth as tools	1. behavioural accommodation may have been required, depending on how quite how limit the individual was in using the affected limb 2. care unlikely	(Condemi et al., 2012)
La Quina, Charente, France, 65,000 BP	La Quina 5/9/ 18 (?)	Adult/ juvenile	tempero-mandibular osteoarthritis, described as very severe	May have compromised chewing and eating and the use of teeth as tools	possibly accommodation and support, such as chewing food and facilitating other activities where the teeth were not required, behavioural modification of the individual likely	(Straus and Cave, 1957)
Les Pradelles (Marillac) France, c. 60,000 BP	Marillac 3	40–60 years, male	Hyperostosis frontalis interna (type B - mild or grade II)	can be asymptomatic but can be linked to headaches and mental imbalance,	likely to be asymptomatic given its moderate nature but may require care if symptoms were present	(Garralda et al., 2014)
Les Pradelles (Marillac), France, c. >58,000 BP	LP femur	adult	Myositis ossificans associated with the linea aspera of the femur	may compromise the function of the affected muscle	given the location, possibly some accommodation linked to mobility	(Mussini et al., 2012)
La Chapelle-aux-Saints, France, 47–56,000 BP	La Chapelle-aux-Saints 1	25–40 years, male	1. Largely edentulous with advanced anterior alveolar infection - may have lost as many as 15 teeth antemortem 2. Abscesses and resorption to right maxilla 3. DJD right mandibular condyle 4. Minimal DJD to occipital condyles 5. Auditory exostoses 6. Pitting and exostoses to left ulna and right humerus 7. osteoarthritis, especially concentrated in the mid to lower cervical vertebrae and upper thoracic vertebrae, described as very severe 8. Severe DJD to spine with schmorl's nodes to C6-C7 and eburnation to some vertebrae and with ossified ligamenta flava	1–4 Pain, compromised mastication and incapacity to use teeth and tools 5. possibly restriction in hearing 6. pain 7–9 Pain and restriction in the range of movement, possibly nerve entrapment or damage 10. pain and restriction of movement while the break heals 11. possibly asymptomatic 12–13 Severe pain and restriction in mobility 14. possibly asymptomatic or pain and limited mobility if severe	1–4 Compromised masticatory apparatus may have required accommodation, both in helping with eating and with allowing other tasks to avoid using teeth as tools 5. likely no accommodation required 7–9 12. long term compromised mobility may have resulted in behavioural modification by the group to compensate 11. likely no accommodation required 13. likely no accommodation required	(Straus and Cave, 1957; Trinkaus, 1985; Tappen, 1985; Dawson and Trinkaus, 1997; Gómez-Olivencia, 2013a,b; Tilley, 2015b)

Table 1 (*continued*)

site and date	specimen	age and sex	pathology	impact	care	references
			9. L4-L5 Baastrup disease 10. Ossification of rib cartilage 11. Break to right thoracic rib broken near the costal cartilage attachment (completely healed) 12. DJD left acetabulum with exostoses and eburnation 13. osteomyelitis and abscess in the left acetabular notch 14. DJD in the toes			
Cove Negra, Valencia, Spain, OIS 3–4, c. 54–51,000 BP	Cova Negra 1	adult	Anterosuperior parietal trauma with external remodeling	possibly pain, bleeding, and short term cognitive impairment	possible short term support linked to the initial trauma	(Lumley, 1975; Arsuaga et al., 2007; Wu et al., 2011a,2011b)
Grotte du Renne, France, c. 50–100,000 BP	Arcy-Sur-Cure 9	Not specified	1. Dental abscess 2. broken teeth	1–2 pain and may compromise mastication and use of teeth as tools for the duration	1–2 compromised masticatory apparatus may have required accommodation, both in helping with eating and with allowing other tasks to avoid using teeth as tools, though only in the short term in this case	(Condemi et al., 2012)
Guattari, Italy, 50–60,000 BP	Guattari 1/ Circeo 1	adult	1. severe periodontal inflammation 2. Edentulous with alveolo-palatal remodeling and atrophied bone, suggesting decreased masticatory function. 3. Periosteal osteophytes present on the palate in a symmetrical pattern along both sides of the medial sagittal line, probable torus palatinus.	1–2 Pain, compromised mastication and incapacity to use teeth and tools 3. likely asymptomatic	1–2 Compromised masticatory apparatus may have required accommodation, both in helping with eating and with allowing other tasks to avoid using teeth as tools	(Sergi et al., 1972)
Forbes' Quarry, Gibraltar, 45–70,000 BP(?)	Gibraltar 1	60s, female	1. Endocranial hyperostosis (warty/nodular type, grade II) limited to the frontal bone, localised to the central portion of the frontal squama 2. Dental abscess	1. can be asymptomatic but can be linked to headaches and mental imbalance, seizures in severe cases 2. pain and may compromise mastication and use of teeth as tools for the duration	1. likely to be asymptomatic given its moderate nature but may require significant care if symptoms were present 2. compromised masticatory apparatus may have required accommodation, both in helping with eating and with allowing other tasks to avoid using teeth as tools, though only in the short term in this case	(Condemi et al., 2012)
La Ferrassie, France, 43–45,000 BP	La Ferrassie 1	>50, male	1. temporomandibular osteoarthritis 2. abscesses in the mandible 3. upper limb fracture 4. healed fracture to the right femoral greater trochanter 5. appendicular symmetrical periostitis (pronounced in the distal femora, proximal tibiae, distal tibiae, distal fibulae) 6. hypertrophic pulmonary osteoarthropathy (likely in the initial stages - estimated 2–14 months duration)	1-2 pain when chewing 3. pain and short term restricted mobility 4. pain and significant disruption to mobility weight bearing structures 5. pain and swelling to the limbs and joints, possibly limiting mobility 6. pain and swelling in the joints and clubbing of the digits, possibly limiting mobility and fine motor skills	1–2 behavioural modification and accommodation in eating and using teeth as tools 3–4 mid term accommodation and care for significant immobility 5–6 long term accommodation	(Straus and Cave, 1957; Fennell and Trinkaus, 1997; Gómez-Olivencia, 2013a,b; Tilley, 2015b; Trinkaus and Villotte, 2017; Gómez-Olivencia et al., 2018)
La Ferrassie, France, 43–45,000 BP	La Ferrassie 2	young adult, female	1. healed fracture of the right tibia 2. fractured fibular diaphysis with infection	1. pain and short term restricted mobility for weight bearing bone 2. pain and short term restricted mobility	1–2 short term accommodation and care in setting the bones	(Heim, 1976; Guérin et al., 2015/6)
Kleine Feldhofer	Neanderthal 1, Feldhofer	50 + years, male			Short term: short term care for lesion on supra-orbital arch?	

(continued on next page)

Table 1 (*continued*)

site and date	specimen	age and sex	pathology	impact	care	references
Grotte, Neander Valley, Germany, c. 40,000 BP			1. fractured left ulna with evidence of ostoclastic processes 2. Atrophy of left humerus and hypertrophy of right humerus 3. chronic sinusitis and osteoclastic processes in the bone 4. lesion to the right supraorbital arch, likely meningitis or trauma and associated with 3. 5. tumorous process associated with 3.	1. painful and with restricted movement in the limb for a number of weeks 1. reduced use of left arm 3. pain due to persistent infection. 4. pain and severe side effects if meningitis 5. potentially benign but would be serious side effects if malignant	Long term: Long term accommodation for limited movement in left arm, probable care for extensive inflammation of sinuses and metastatic disease leading up to death	(Schmitz et al., 2002; Schultz, 2006; Cowgill et al., 2015)
Saint-Césaire, layer E_{JOP}, France, c. 36,000 BP	Saint-Césaire 1	young adult, male	Fractured skull from a wound that penetrated the internal lamina, with evidence of healsing	Pain, heavy bleeding, and short term cognitive impairment, with penetration of the internal lamina increasing the risk of infection	the location of the wound suggests help in dressing and cleaning the wound may have been required over a short term period	(Zollikofer et al., 2002)

Fig. 1. Sites with Neanderthal skeletal material and key sites with probable evidence of recovery through care. Healthcare case studies (see Table 1) are in red and numbered: 1) Forbes' Quarry, 2) Cova Negra, 3) Les Pradelles, 4) La Quina, 5) La Ferrassie, 6) Regourdou, 7) La Chapelle-aux-Saints, 8) Zeeland Ridges, 9) Kleine Feldhofer, 10) Arcy-sur-Cure, 11) Bau de l'Aubesier, 12) Saint Césaire, 13) Riparo Mezzena, 14) Guattari, 15) Krapina, 16) Šal̆a, 17) Kiik-Koba, 18) Shanidar. Neanderthal skeletal material (black) is compiled from Nespos and (Diedrich, 2014) with additions). Symbols: ▼ cranial/dental material only ▲ postcranial material only · ● near complete or partial skeleton.

diseases) are identified in skeletal material for example, and of these only the most severe cases can be attributed to probable care from others with any confidence. Equally many injuries or illnesses which are life threatening without moderate care leave no palaeopathological signature in skeletal material. These could include healthcare that allows rest by provisions of food, water or warmth or by prevention of deteriorations (e.g. wound cleaning). Costly cases of care are highly visible archaeologically whilst more common care for moderate injuries and illness are largely invisible. The visible archaeological evidence for care is best understood as the 'tip of the iceberg' of practices of healthcare which would have been predominantly low cost, highly effective and adaptive in improving health and reducing mortality.

A predominance of minor injuries and illnesses and an overall adaptive value of even modest healthcare practices in modern contexts illustrate that typical healthcare is likely to have taken the form of a low cost and highly effective response to minor injury and illness. The profile care needs in modern wilderness activities is one in which severe trauma is very rare, and medical attention is typically focused on sprains and strains, particularly of the lower body, followed by moderate illnesses such as gastrointestinal complaints for example (McIntosh et al., 2007) (Fig. 2). Minor

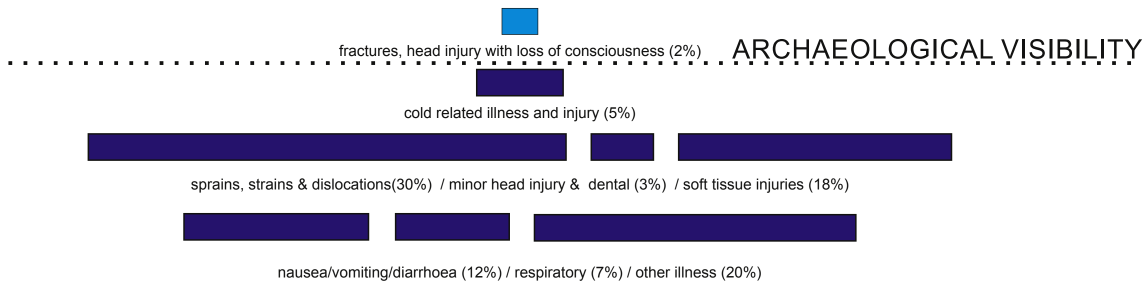

Fig. 2. Medical treatment in wilderness locations. National Outdoor Leadership school's incidents requiring medical attention in wilderness activities in Wyoming, Alaska, Arizona, Washington, Idaho, Mexico, Chile and the Yukon Territory 1051 individuals (average age 22 years) 1998–2003 (data from McIntosh et al., 2007).

injuries, such as sprains, strains and lacerations which nonetheless require rest and treatment are by far the vast majority of injuries and illnesses which require some form of healthcare in active outdoor occupations across a range of modern contexts ranging from general athletics injuries (DeHaven and Lintner, 1986), to those sustained by paramedics (Maguire et al., 2005) to injuries seen in big game hunters (Lambrecht and Hargarten, 1993; Reishus, 2007), expeditions in extreme environments (Heggie and Küpper, 2018) or extreme sports such as rodeo riding (Griffin et al., 1987; Stoneback et al., 2018). 96% of the injuries requiring medical attention in wilderness activities, mostly through hiking with a heavy pack, were moderate (such as sprains and minor lacerations) and only 4% severe, such as fractures (of 633 cases) (Leemon and Schimelpfenig, 2003). In the anatomical record of injuries recorded in palaeolithic material in contrast (Wu et al., 2011a, 2011b) almost all would be classed as 'severe', taking the form of fractures and head injuries, whilst far more common and much less serious pathologies are largely invisible.

A profile of frequent injury and ill health, and predominantly small scale but effective care for the ill and injured is also typical of modern hunter-gatherer contexts. Amongst the modern Ache of Paraguay for example adult males were typically too sick or injured to hunt on 21% of 470 man days reported, being provisioned or cared for due to what are mostly moderate illnesses or injuries (Gurven et al., 2000; Hill and Hurtado, 2009). Pre contact populations experienced similar rates of ill health (Hill and Hurtado, 2009). Likewise records illustrate that between 1981 and 1982 men amongst the Efe of the Ituri forest were also ill or injured 21% of the time (Bailey, 1991). Vulnerable and ill members of modern hunter-gatherers groups are thus routinely provisioned when in need, much in the same way as with vulnerable young. Sometimes runs of ill health requiring provisioning and care to aid recovery can be lengthy. For the Ache during the same period runs of being debilitated through ill health lasted at least 30 days in 40% of cases (Hill and Hurtado, 2009, 3865). 75% of Tsimane adults had been incapacitated by illness or injury in the past three months (Hill and Hurtado, 2009, 3865), and 42 of the 49 men in the Arroya Bandera Ache experienced at least one 90 day period with no meat acquisition in a seven year period, largely due to ill health (Hill and Hurtado, 2009). Amongst the Shiwiar forager-horticulturalists around 50% of adults had been incapacitated and unable to forage for at least a month due to illness or injury and would not have survived without care from others (Sugiyama, 2001, 2004). Small investments in care, such as wound cleaning and provisioning significantly reduce the risk of more severe conditions developing which might further affect health, whilst moderate investments in healthcare can play an important role in reducing mortality. Rather than being costly in adaptive terms, most instances of Neanderthal healthcare are likely to have been low cost and highly effective in reducing mortality risk.

Even low cost and short term healthcare practices have important evolutionary consequences through altering differential survival from injury and illness. Healthcare provisioning as an adaptation may have a long evolutionary history, with simpler forms of more immediate care in earlier species potentially providing the basis for the more sustained and knowledgeable care seen in Neanderthals.

2. Healthcare provisioning in long term evolutionary context

Whilst Neanderthals are the pre-modern human for which we have the most extensive evidence of healthcare practices, care for the ill and injured, albeit in simpler forms than those seen in Neanderthals, is recorded in much earlier species, and even in highly social and collaborative mammals more broadly. Both the behavioural ecology of care for the ill and injured in other species, and archaeological evidence for healthcare prior to archaic humans argue for a long term adaptive function to such practices.

2.1. Care for the ill and injured in non-human primates and social mammals

Whilst care for the ill and injured is often portrayed as uniquely human, such care is also recorded in both non-human primates and in social mammals in general. Examples of short term care for ill or injured peers are seen in non-human primates, particularly apes, and range from tending wounds (Fabrega, 1997; Hart, 2011; Fashing and Nguyen, 2011) to more complex practices such as birth assistance (Demuru et al., 2018). These behaviours fit within primate and ape tendencies to respond to distress through consolation as well as capacities to help in a targeted way (Romero et al., 2010; Clay and de Waal, 2013; Pérez-Manrique and Gomila, 2017). Other mammals also demonstrate care practices. Dolphins will support an injured group member at the surface to allow them to breathe for example, and elephants will also protect and lift injured members of the group (Pérez-Manrique and Gomila, 2017). It is in highly social mammals outside of the primate order, and particularly in social carnivores where we see the most widespread evidence of *long term care* for illness and injury however. Wolves can provision ill group members by regurgitating food for example (Barber-Meyer et al., 2016), and in one instance a lioness was provisioned for eleven months while severely injured (Schaller, 2009; Hart, 2011). Provisioning of the ill and injured and their survival from what might otherwise have been injuries bringing a high probability of mortality is recorded in highly social mammals as diverse as lions, wolves and mongooses (Rasa and Anne, 1983). Common proximate mechanisms in which mammalian pro-social responses to infant distress are extended to adult group members are likely to explain these similarities (Decety et al., 2012, Decety et al., 2016). The importance of behavioural systems in ethological theory give at least one possible explanation for how instinctive attachment behaviours that promote survival may be linked to behavioural care-giving systems (see Leedom, 2014).

The most probable evolutionary *explanation* for apparently 'selfless' care of adult group members lies not only in the benefits of helping relatives but also the selective advantages of reducing the risk of mortality of other group members in situations where groups are highly interdependent (Frank and Linsenmair, 2017). The selective benefits of care for the ill and injured are clearest where groups consist of close relatives. However where the survival of any one member is strongly linked to that of the others in the group caring for those who are injured is still selectively advantageous even without a high degree of genetic relatedness.

Care for the ill or injured in hominins, whilst seen as marking a distinctive human evolutionary threshold, is in fact not surprising when considered within this broad comparative evolutionary context. It has become increasingly clear that collaboration was essential to early human adaptation for example. From direct reciprocity common in primates human adaptation becomes increasingly dependent not only on indirect but also generalised reciprocity, with reputation for example likely to have played a key role in social dynamics (Manapat et al., 2013; Jordan et al., 2016; Steinkopf, 2017). As soon as collaboration became essential for survival, and individuals within any group highly interdependent, then selective pressures leading to care for ill and injured group members are likely to have been increasingly significant, alongside distinctive social pressures emerging from trust and reputation (Spikins, 2015, 2012; Steinkopf, 2017). Care for the ill and injured would thus be expected to have emerged in hominins alongside other forms of collaboration such as collaborative parenting of increasingly vulnerable young, collaborative defence from predators, increased meat eating, food sharing, collaborative hunting and increased dependence on social learning (Fuentes et al., 2010; Burkart et al., 2017). Rather than see these adaptations as separate responses, these different behavioural traits are perhaps best seen in terms of broader 'health sharing', in which risks to health or energetic costs are expended on behalf of others in the context of broader evolutionary advantages of proximate acts of altruism (Marsh, 2016; Hare, 2017).

2.2. Archaeological evidence for care for the ill and injured in early hominins

Unsurprisingly some of the earliest widely accepted evidence for care for illness and injury dates to precisely the time at which major changes in pro-social collaboration appear to be taking place in human evolution, ie around the emergence of Homo. Examples include the probable care for a hominin from Dmanisi with tooth loss and periodontal disease dated to 1.8 million years ago (Lordkipanidze et al., 2005; Trinkaus and Villotte, 2017), for KNM-ER 1808, a *Homo ergaster* with hypervitaminosis A or treponemal disease (Walker et al., 1982; Skinner, 1991; Doolan, 2011) dated to around 1.6 million years ago, and for WT1500, a *Homo erectus* with juvenile disc herniation dated to 1.6 million years ago (Haeusler et al., 2013; Schiess et al., 2014). Earlier *potential* examples of care have however also been proposed in australopithecines such as a probable *Australopithecus africanus* from Sterkfontain in South Africa (Stw 363), dated to around 2–2.5 million years ago with severe damage to the foot (Pickering and Kramers, 2010; Fisk and Macho, 1992) and an *Australopithecus sediba* juvenile from Malapa (MH1) dating to around 2 million years ago with a bony tumour of the spine which would have limited movement and caused chronic pain and muscle spasm (Randolph-Quinney et al., 2016).

Care for the ill and injured in early hominins may also have been under particular selection pressures unique to hominins themselves, quite apart from more general pressures on pro-social collaboration seen in other mammals. In comparison to other primates early hominins would have been unusually vulnerable to predation as they moved into more predator rich open environments, whilst lacking evolved defences to this type of predation. Moreover entering competition for scavenged and hunted food with other predators would also increase the risk of injury (Brantingham, 1998). Injuries are well attested in hominins from the australopithecines onwards, deriving from factors such as falls (L'Abbé et al., 2015), predator attacks (Berger and McGraw, 2007; Pickering et al., 2004), encounters with prey and competition with other carnivores (Pickering et al., 2004). A reliance on obligate bipedalism will have made lower limb injuries a particularly high mortality risk for early hominins. Furthermore an increasingly lengthy period of infant dependency will have represented greater losses of investments if succumbing to mortality through injury or disease before reaching reproductive age. Added to which a co-evolution of diseases *with* healthcare practices might lead to evolved reliance on healthcare as hominins developed reduced resilience in the presence of care (Hart, 2011; Kessler et al., 2017).

The particular circumstances affecting the selection pressures on hominins to reduce the risk of mortality from injury make direct comparisons with apparently notable *independent* recovery from illness and injury in non-human primates problematic (Spikins et al., 2018). Whilst such comparisons are commonly seen as suggesting that hominins may have survived even remarkable trauma without care (DeGusta, 2002), non-human primates are able to rely on a forelimb to replace the function of an injured rear limb to move around, and able to use a rear limb to replace an injured forelimb when foraging. In this way injured primates can often forage independently despite injury even though their foraging efficiency is reduced, and for this reason injured chimpanzees can often survive despite injured limbs (Munn, 2006). The case of a one armed gibbon able to brachiate effectively by using a rear limb as an 'arm' (Sayer et al., 2007) is a particular case in point. However as obligate biped hominins could not replace an injured rear limb with a forelimb in order to move around effectively, and rear limbs become far less manipulative and increasingly less helpful as a replacement for a forelimb particularly given an increased reliance on tools. Moreover as the diet of early hominins became more dependent on collaborative scavenging and hunting (Domínguez-Rodrigo et al., 2014), foraging independently despite injury would be less viable than it is in other primates, particularly in a context with high rates of predation. In comparison to non-human primates hominins would have been more prone to injury, have a higher risk of mortality from injury and been less able to recover independently or find sufficient resources alone.

Increasing dependence on collaborative hunting in later hominins, particularly in unpredictable environments, is likely to have placed further selective pressures on healthcare as a means of reducing mortality risks. Care appears to have been common in *Homo heidelbergensis*/pre-Neanderthal populations in Europe at Sima de Los Huesos around 350,000bp for example. Amongst around 28 individuals interred in a mortuary pit, several provide evidence for care or accommodation. Craniosyntosis in a young child which did not adversely affect her care, despite physical deformity (Gracia et al., 2009) has attracted a certain amount of attention. This case may not be particularly surprising however as this condition does not always affect cognition and behaviour, and care for even extremely disabled infants is known in non-human primates (Matsumoto et al., 2016). However another individual suffered from deafness, probably due to infection (Pérez et al., 1997; Trinkaus and Villotte, 2017), which is likely to have needed accommodation from others. Perhaps most notably an elderly individual is likely to have walked with the aid of a stick, with his support likely to have involved a level of planning around his lack of mobility (Bonmatí et al., 2010, 2011).

Both general pressures common to highly social collaborative mammals, as well as selective pressures unique to hominins, will have made healthcare provisioning an increasingly adaptive response to mortality risks from injury, and in turn healthcare provisioning will have influenced the ecological niche which hominins could occupy. Moreover in hominins memory, long term planning and accumulated knowledge and understanding become increasingly evident in healthcare, much as in other complex behaviours such as collaborative hunting.

In the case of Neanderthals a combination of ecological factors may have made care particularly essential to survival.

3. The ecological challenges faced by Late Pleistocene Neanderthals

3.1. Occupying challenging environments in the North Temperate zone

Neanderthals occupied what was at the time a northernmost extension of archaic human occupation, being present in Western Eurasia from approximately 250ka BP (Marra et al., 2017). Securely dated evidence for Neanderthal occupation stretches as far north as 55° N (Finlayson and Carrión, 2007; Slimak et al., 2011; Nielsen et al., 2017) although highly debated Mousterian assemblages have been found as far north as near the Arctic Circle at Byzovaya (Slimak et al., 2011). As descendents of earlier european *Homo heidelbergensis* and pre-Neanderthal populations Neanderthals were not the first hominins to successfully occupy Western Eurasia but they nonetheless occupied the most northerly regions.

In general ecological terms as environments become cooler, more seasonal and often more arid with increasing latitude (or altitude, or effective latitude during glacial phases), survival becomes increasingly dependant on abilities to cope with the challenges imposed by the environment rather than biotic interactions. Both intra and interspecies competition is affected by this latitudinal gradient (Schemske et al., 2009). Thus survival depends on managing and mitigating the notable risks which these environments bring, particularly at the most northerly limits of occupation and during glaciations where effective latitude (in terms of cold and aridity) increases. With increasing latitude resources become more variable seasonally, increasingly patchy and less reliable placing a challenge on hominin occupation (Pearce et al., 2014). Risks to mortality and survival come from several different sources. There are risks to effective reproduction posed by seasonal variations in the resources needed to support pregnancy and lactation for example, variable resources leading to potential famines, extremes of cold which can threaten infant survival, as well as high requirements for mobility to exploit more patchy resources. Dependence on animal food for survival increases with increasing distance from the equator (Johnson, 2014), and moreover average prey size increases with cold and increasing latitude (Rodríguez et al., 2008) bringing elevated risks of injury and mortality through injury from hunting as well as through competition with other predators.

Human health, disease and mortality risk in modern ethnographic contexts is strongly correlated with observed changes in ecology occurring with variations in latitude and aridity (Waguespack, 2002; Kelly, 2013, 200). In warmer and more equatorial environments the risk of mortality from pathogens as well as the health effects of pathogen loads are highest, both due the diversity of pathogens present and to a greater population density of hosts and greater possibilities for transmission. Hot and humid environments are particularly favourable for the spread of pathogens which are commonly the primary cause of hunter-gatherer mortality (Froment, 2001) and continue to influence life history and development in modern contexts in complex ways (Magid et al., 2018). As environments become more cold and seasonal with increasing latitude the mortality risk from pathogens reduces. The risks posed by any possibilities of pathogen transmission from healthcare practices also reduce. However, as risks of infectious diseases reduce with increasing latitude, mortality risks from cold, injury and famine rise significantly. For modern Inuit for example the major risks to mortality come from cold, injury and famine, with injury deriving not only from hunting and mobility in difficult terrain but also from the effect which high endurance demands have on wear and degeneration of bone. Around 50% of Inuit from northern Alaska, Canada and Greenland, both historically and in archaeological contexts have spondylitis of the spine due to fatigue and stress fractures for example (Merbs, 2002). Moreover hunting accidents caused 15% of the deaths of an ethnographically documented southern Baffin Island group (Mcelroy et al., 2009) despite complex weaponry. In these cooler and more arid environments, healthcare practices are more focused on treating injuries, which both demands more technical knowledge and has greater returns in terms of recovery than the treatment of pathogens and infectious disease. Simply occupying cold and more arid environments elevated mortality risks from injury compared to those experienced by the distant ancestors of Neanderthals in Africa and Asia.

The highly seasonal, risky and unpredictable nature of Late Pleistocene environments presented major ecological challenges for human communities. Palaeoecological evidence documents a notable instability in European temperatures, with several harsh climatic events concurring to create a notable deterioration of an already severe glacial environment (Sánchez Goñi et al., 2002; Moreno et al., 2014). During the Last Glacial period a series of Heinrich events, during which large icebergs traversed the North Atlantic causing global climate cooling, followed by rapid warming episodes (ie Dansgaard-Oeschger events) caused abrupt alternations of cold-arid and warm-humid environments. Moreover extended and independent phases of regional drought with significant repercussions on Neanderthal populations have been documented (Luetscher et al., 2015; Wolf et al., 2018). Climatic and ecological challenges at less than millennial scale had a substantial impact on Neanderthal communities during MIS 3, affecting the availability of food resources, changing distributions of plant and animal communities, and forcing costly and repeated mobility and changes in dietary habits (Hodgkins et al., 2016; El Zaatari et al., 2016). Furthermore there were notable contractions of occupation from north and east Europe and into a few regions with milder climates including southerly Mediterranean refugia (Finlayson et al., 2006; Stewart et al., 2010). There was also a significant fragmentation of Neanderthal distribution and demographic decline in Europe with frequent regional extinctions (Dennell et al., 2011; Sánchez-Quinto and Lalueza-Fox, 2015; Hublin and Roebroeks, 2009; Benito et al., 2017; Wolf et al., 2018) and sporadic population replacement (Fabre et al., 2009; Dalén et al., 2012; Melchionna et al., 2018; Hajdinjak et al., 2018). The unreliability of food resources will have also affected populations in other ways. Evidence for nutritional stress from enamel hypoplasia amongst Neanderthals is common and within the upper range of that observed within modern hunter-gatherers for example (Ogilvie et al., 1989; Guatelli-Steinberg et al., 2004; Hlusko et al., 2013). Furthermore contacts between groups may have been limited by low population density (see Dennell et al., 2011; Bocquet-Appel and Degioanni, 2013; Sánchez-Quinto and Lalueza-Fox, 2015; French, 2016; Simons and Sella, 2016; Hajdinjak et al., 2018), driven by low plant productivity and animal biomass, and the energetic costs of movement across large areas of landscape. Low population densities and limited contacts also explains low rates of introgression, with half sibling matings being common (Prüfer et al., 2014; Castellano et al., 2014; Rogers et al., 2017; Harris and Nielsen, 2016).

Some Neanderthal populations undoubtedly occupied relatively stable and productive ecological regions, particularly in Mediterranean contexts, however for many this was survival 'on the edge'. Although the arrival of anatomically modern humans has been suggested as one obvious possible factor in eventual Neanderthal demise (Errico and Sánchez Goñi, 2003; Hortolà and Martínez-Navarro, 2013) and it may have been precisely the challenges posed by climate and environmental changes which were ultimately the most significant influence (Finlayson et al., 2004; Stewart, 2007; Müller et al., 2011/2; Melchionna et al., 2018) or at least a combination of several factors including within them environmental and ecological changes (Rey-Rodríguez et al., 2016). The contemporary extinction of around 35–40% of co-existing megafaunal species in particular supports the argument of a primary role of environment in Neanderthal decline (Stuart and Lister, 2012) with Neanderthal populations eventually dying out in most of Europe between 35 and 40 ka BP (Higham et al., 2014; Hublin, 2017) and ultimately in Iberia (Finlayson et al., 2006).

3.2. Biological and anatomical responses

The effects of selection pressures from challenging environments on Neanderthal biology and anatomy are well accepted. High endurance requirements and frequent famines influenced their body shape, proportions and physiology for example. A similar body shape to other populations adapted to cold environments has been noted for some time (Ruff, 1994; Holliday, 1997) and their facial morphology may also be an adaptation to cold and high energy demands (Wroe et al., 2018). A large thorax may be an adaptation to enhanced physical activity (García-Martínez et al., 2014) and likewise physiological adaptations to conserve resources appear to be an adaptation to highly seasonal resource availability and frequent famine (Vernot and Akey, 2014; Sankararaman et al., 2016). Furthermore cognitively Neanderthal's large visual cortex may also be an adaptation to selective pressures on identifying and hunting animals in conditions of potentially low visibility (Pearce et al., 2013).

3.3. Adaptive subsistence practices

Neanderthals also adapted their subsistence practices to the ecological contexts, with Neanderthal diets widely acknowledged as reflecting their ecological circumstances. Neanderthals occupied regions with substantial ecological variation in time and space, and varying their diets accordingly (Fiorenza et al., 2011; El Zaatari et al., 2016). Though famously characterised as hunters of big game Neanderthal diets were clearly far more complex and variable. Plant foods appear to have been exploited as and when available and are likely to have formed some component of diets throughout the region occupied (Henry et al., 2011; Power et al., 2018). Coastal populations would have been able to rely on less risky marine and intertidal resources, as seen at Gibraltar in the exploitation of shellfish and seals (Cortés-Sánchez et al., 2011). Fish and birds are also likely to have been exploited when available (Hardy and Moncel, 2011). In some Mediterranean regions, particularly in interglacial periods, it would even have been possible to depend significantly on plant resources (Salazar-García et al., 2013), and Neanderthals appear to have particularly flourished in these environments (Benito et al., 2017). At El Sidron the dietary profile from dental calculus suggests that a notable component of plant foods contributed to Neanderthal diets for example (Weyrich et al., 2017; Estalrrich et al., 2017). Neanderthals in Mediterranean contexts provide the only known cases of dental caries due to ingestion of carbohydrates in the form of plant resources (Walker et al., 2011).

There is however good evidence for a heavy dependence on a largely meat based diet in most regions alongside behavioural adaptations to a dependence on large mammals for subsistence. Stable isotope studies (Bocherens et al., 2005; Richards and Trinkaus, 2009; Naito et al., 2016), molar macrowear (Fiorenza et al., 2011; El Zaatari et al., 2016; Estalrrich et al., 2017) and faecal biomarkers (Sistiaga et al., 2014) suggest that Neanderthals outside of the Mediterranean region depended on a largely meat based diet. Faunal remains on archaeological sites also suggest a reliance on large game, which varied according to the ecological context, with bison, reindeer and horse predominating within faunal assemblages (Smith, 2015), though Neanderthals also exploited megafauna in the form of woolly rhinoceros and mammoth, such as at La Cotte de St Brelade (Scott et al., 2015). They were clearly well able to adapt to the different opportunities which large game provided, sometimes hunting individual animals, and at other times focusing on herds, including the hunting of prime age individuals. At Jonsac (Niven et al., 2012) and La Pradelles (Rendu et al., 2012) hunting seems to have focused solely on reindeer for example.

That the pressures of reliance on meat from large game animals were a pressing adaptive problem in many regions is clear. Whilst plant foods and other resources were undoubtedly a component of diets everywhere, meat as the dominant resource outside of the Mediterranean region, and probably to the most extreme degree in late winter and early spring imposes physiological challenges. In open environments, as recorded at Spy, Neanderthals survived on a largely carnivorous diet for example (Weyrich et al., 2017; Estalrrich et al., 2017). A high protein diet can have serious physiological consequences (Hardy, 2010; Hockett, 2012; Fiorenza et al., 2015) as is clear from palaeopathologies in Inuit populations (Bishop, 2011) which include anaemia in the context of high consumption of meat (Jamieson and Kuhnlein, 2008). Likewise a Neanderthal infant from Kiik-Koba appears to have been a victim of vitamin C deficiency for example (Mednikova, 2017). What plant materials and fats were available are likely to have been important. Mammoths may have provided important fat from their brain material for example (Agam and Barkai, 2016) and Neanderthals may also have diversified their diet by eating vegetable matter from the stomachs of their prey (Buck and Stringer, 2014). Selective pressures to adapt to the strains imposed by a high protein diet has also been argued to be the explanation for the large lower thorax of Neanderthals (Ben-Dor et al., 2016).

Individual and group survival clearly depended on capacities to adapt to notable ecological challenges, and to find ways to reduce risk, with healthcare practices best seen as part of these wider patterns of adaptation.

4. Neanderthal healthcare provisioning as adaptation

4.1. Subsistence related mortality risks

Selective pressures to reduce mortality risks through healthcare provisioning come most obviously from the demands of common subsistence practices.

Given that most available biomass was in the form of large herbivores in many regions (Daura et al., 2017) a common reliance on hunting large game would clearly be an inevitable part of Neanderthal adaptation in many contexts. Requirements for high levels of mobility driven by relying on highly dispersed game (Niven et al., 2012) bring risks of injury in itself, alongside simply

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moving across difficult terrain (such as when hunting ibex, (de los Terreros et al., 2014; Yravedra and Cobo-Sánchez, 2015). However it would have been Neanderthal hunting methods which brought particular injury risks. Close range hunting with wooden or stone tipped spears seems to have been the norm given environments in which ‘running down’ prey through heat exhaustion would not have been a feasible strategy (Rhodes and Churchill, 2009; Shea and Sisk, 2010). Hunting of any animal prey is dangerous, however close encounter hunting of large game demands a high level of collaboration and brings particularly high injury risks (Gaudzinski-Windheuser et al., 2018). Evidence from characteristic impact patterns on fallow deer at Neumark-Nord during the Last Interglacial confirms the use of close range spears (Gaudzinski-Windheuser et al., 2018). A combination of thrusting and close range throwing seems the most likely hunting technique as Neanderthals would have been physically capable of using thrown projectiles (Roach et al., 2013). Repeated throwing behaviour is also the most likely explanation for humeral abnormalities in a Neanderthal from Tourville-la-Riviere (Faivre et al., 2014).

Neanderthal's lack of projectile technology has been seen as a potential adaptive disadvantage (Shea and Sisk, 2010). However, close encounter hunting, taking advantage of landscape features, despite the high rates of injury, may simply have been the most effective hunting method for the faunal communities which Neanderthals exploited. For many of the larger species exploited by Neanderthals neither long distance spears nor even bow and arrow technology would have had the kinetic energy required to sufficiently pierce skin and flesh. For larger body size prey hand delivered spears and use of physiographic features are the typical means of hunting in modern hunter-gatherer contexts (Churchill, 1993), as well as many Upper Palaeolithic contexts such as archaic period bison hunting sites in North America. Close encounter hunting, using landscape features against which to drive animals explains patterns of mammoths and woolly rhinoceros exploited by Neanderthals at La Cotte de St Brelade (Scott et al., 2015). Neanderthals also exploited game which were dangerous to exploit in other ways, such as ibex (*Capra ibex*) and chamois (*Rupicapra rupicapra*), found in particularly difficult terrain (de los Terreros et al., 2014; Yravedra and Cobo-Sánchez, 2015).

The elevated injury rates from close range hunting compared to the use of long range projectiles is evident in ethnographic and archaeological contexts for example (Churchill, 1993). Amongst neighbouring prehistoric groups at Point Hope Alaska, the Tigara, reliant on close encounter hunting of bowhead whale, had twice the rates of severe injury than the Ipiutak who were reliant on projectile hunting of caribou (22% vs 12% of skeletal remains showing traumatic injury) (Dabbs, 2011). The faunal communities of Late Pleistocene Western Eurasia also brought additional mortality risks for which we have no modern analogues. The megafauna present during Neanderthal occupation, including mammoths and woolly rhinoceros would be particularly dangerous prey, easily able to overcome an individual human assailant.

Besides direct confrontations with prey Neanderthals also faced the presence of large carnivores which in turn were dangerous as competitors and as predators and for which we have no modern analogues (Wang et al., 2004). Spotted hyenas (*Crocuta crocuta*), cave lions (*Panthera spelaea*) and cave bears (*Ursus spelaeus*) would have been the most common large carnivore threats, due to their overlapping habitats and prey choices (Ardèvol and López, 2009; Blasco et al., 2010; Dusseldorp, 2011). Dangerous encounters with leopards (*Panthera pardus*) and wolves (*Canis lupus*) seem to have been less frequent (Camarós et al., 2017). Unfortunately, it is not an easy task to determine from the archaeological record whether the carnivore damage discovered in several sites are the result of scavenging activity or from a direct confrontation, but the latter is reliably recognised in several cases (Fernández-Lomana et al., 2010; Camarós et al., 2016a, Camarós et al., 2017). Conflicts with such predators were extremely dangerous and could lead to death or severe injuries, as also demonstrated by forensic studies on current-day carnivore attacks (Camarós et al., 2016a). The effects of carnivore attacks can be significant and in modern contexts are more likely to lead to mortality in women and children (Treves and Naughton-Treves, 1999).

Interactions between hominin and large carnivores will have occurred in a variety of contexts, and across the whole range of Neanderthal occupation, not only through competition for resources, but also potential occupation sites in caves (Conard, 2011; Stiner, 2012; Camarós et al., 2016b; Camarós et al., 2017). Neanderthals occupied cave sites also favoured by carnivores, with faunal accumulations in these locations deriving from both (Rufà et al., 2017). Cave bears often occupy caves also frequented by Neanderthals, such as in the Swabian Jura for example (Conard et al., 2012). Neanderthals may have been unlikely to have been a chosen prey, with other animals bringing a lower risk of mortality and it also seems unlikely that large carnivores were hunted to obtain hides (Camarós et al., 2016b) or to produce bone ornaments and bone tools (Abrams et al., 2014; L. Niven, 2006). Nonetheless close interactions with large carnivores brought considerable injury risks (Camarós et al., 2016b).

Theoretically at least the distribution and character of injuries across the skeleton may be a potential source of evidence for the relative injury risks from different activities. A greater prevalence of injuries to the head and upper body in Neanderthal skeletal material appeared to be similar to that seen in adult rodeo riders and supported an interpretation of the majority of injuries being sustained through direct engagement with large and dangerous prey (Berger and Trinkaus, 1995). This interpretation remains debated however (Trinkaus, 2012). Different physiologies make such comparisons difficult, particularly as the injury profile in adolescent rodeo riding is notably different (Stoneback et al., 2018). Furthermore similar injury profiles also characterise pathologies in skeletal remains throughout the Pleistocene (Wu et al., 2011a, 2011b) suggesting that differential preservation may be a more likely explanation for this pattern.

The extent to which any particular individuals may have been protected from the mortality risk imposed through hunting large game and competing with large carnivores, or indeed differentially exposed to such risks, also remains unresolved. Inexperienced adolescents are likely to have been at particular risk of injury in close encounter hunting, with their loss particularly costly in terms of energetic investments against future returns. Whether Neanderthals had a gender based division of labour also remains an area of debate (Kuhn et al., 2006; Balme and Bowdler, 2006; Estalrrich and Rosas, 2015). A gender based division of labour exists in modern ethnographic contexts, however this does not preclude women's hunting and women in many such contexts are expert hunters, albeit of smaller and less dangerous game than men (Goodman et al., 1985; Kelly, 2013). However women may equally have been more involved in hide preparation, as suggested by dental wear studies (Estalrrich and Rosas, 2015). The reduced mobility of a pregnant female from Isernia inferred from strontium isotope studies (Lugli et al., 2017) suggests that pregnant women (perhaps alongside infants and the injured) may have been protected from the costs of travelling long distances in search of food resources, and perhaps also mortality risks from hunting. Nonetheless some involvement of females as well as males in dangerous hunting has been argued to explain the limited evidence for similar injuries across both genders (Kuhn et al., 2006).

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4.2. Mortality risks from interpersonal violence

Further mortality risks may have been driven by interpersonal violence. Lethal interpersonal violence has been recorded in pre-Neanderthal populations at Sima de los Huesos where cranium 16 shows evidence of several blunt force trauma blows to the frontal bone for example (Sala et al., 2015). For Neanderthals themselves there are two recorded instances of probable interpersonal violence, one individual from St Cesaire (Zollikofer et al., 2002) and one from Shanidar (Shanidar 3) (Churchill et al., 2009b). The former suffered a blunt force head wound (from which they recovered) and the latter a projectile point injury, most probably from modern human projectiles, which appear to have led to death several days later. Interpersonal violence has also been argued to be the most likely explanation for patterns of cranial trauma at Krapina (Estabrook and Frayer, 2014) although other instances of potential interpersonal violence are more ambiguous. Although patterns of subsistence activity in modern hunter-gatherers can be relatively predictable from ecological context their rates of violence are however notoriously variable. Some hunter-gatherer groups having no recorded cases of interpersonal violence whilst violence is far more frequent in other contexts (Hill et al., 2007; Wrangham et al., 2006; Lee, 2014; Lomas, 2009). Thus there may have been no single pattern over the long period and large spatial extent of Neanderthal occupation. Moreover very low population densities (Bocquet-Appel and Degioanni, 2013; Sánchez-Quinto and Lalueza-Fox, 2015) would argue against any significant territorial aggression (it would be quite simply impossible to 'police' a territory and accidental encounters with other groups would be rare) whilst high genetic relatedness (Prüfer et al., 2014; Harris and Nielsen, 2016) argues against excessive intragroup aggression. The contribution which social factors may have made to injury risks thus remains far less clear than those factors related to ecology and subsistence.

4.3. The influence of Neanderthal behavioural ecology

A certain 'ratchet effect' of increasing dependence on healthcare driven by Neanderthal behavioural ecology may have also have come into effect. Most obviously Neanderthal robust body sizes and high energy requirements (Churchill, 2014) will have placed additional pressures on ensuring adequate resources through hunting success. These same high energy requirements will also have limited group sizes and so increased interdependence, and the significance of any individual mortality to survival. Evidence from El Sidron of a group apparently made up of around thirteen individuals, three related males, four females, three adolescent boys and three infants is one potentially good example (Lalueza-Fox et al., 2011). The loss of even one adult hunter in such a circumstance may be enough to make any such group vulnerable, whilst their high relatedness would act to increase the selective advantages of helping others in the group. High levels of relatedness, with half sibling matings common (Prüfer et al., 2014), also brings with it other pressures on healthcare provisioning. Low genetic fitness, caused by high levels of inbreeding (Sánchez-Quinto and Lalueza-Fox, 2015; Simons and Sella, 2016) brings higher incidences of pathologies which are likely to have required care and support (Dean et al., 2013; Juric et al., 2016; Simons and Sella, 2016). Whether prion diseases from cannibalistic practices added to the disease load remains unclear (Mead et al., 2003). Neanderthals may have become progressively more adapted to a niche in which they may have *depended* on healthcare provisioning.

A particular dependence on the high levels of skill and the technological competence required in acquiring difficult resources in colder and more seasonal environments (Bamforth and Bleed, 1991; Bleed, 1986) will also have increased the advantages of survival of older and even partially disabled group members to Neanderthals. Hunting efficiency, and thus resource acquisition, increases with age in modern hunter-gatherer contexts even where prey are not particularly dangerous (Walker et al., 2002), and this 'learning curve' is likely to have been even steeper for Neanderthals, particularly where variable environments also adds to the relative advantage of knowledge built up over long periods. The knowledge, skills and experience required both in healthcare in general and in care related to assisting births, and keeping babies and infants alive in cold conditions should also not be underestimated. By extending life expectancies through healthcare following injuries the group knowledge and experience of how to deal with many different challenges, particularly in difficult or unusual circumstances, would have increased. Moreover any increased dependence on the knowledge of older members with the greatest life experience would have made care practices all the more necessary to survival.

Whilst subsistence practices may be the most obvious factor influencing pressures to manage mortality risks, clearly various other influences deriving from biological and behavioural adaptations may also have been significant. From the more obvious factors of hunting large and dangerous mammals and moving through cold and difficult terrain, to less immediately evident pressures to maintain skilled hunters in populations and to protect vulnerable young a combination of factors may have put particularly acute selection pressures on means of reducing morality risk in Neanderthals (see Table 2).

From relatively minor and short term care of sprains, lacerations, minor illnesses or births, to more demanding care for more severe or long term conditions, we argue that healthcare will have had a significant impact in allowing Neanderthals to 'live to fight another day' and continue to contribute to group survival. Given that Neanderthals often lived 'on the edge' of viable long term occupation in many regions their elevated mortality risks may have been unsustainable without such care.

4.4. The comparative ecological context

Further support from the role of healthcare in reducing mortality risks in Neanderthals comes from a comparative ecological context. Whilst the ecological significance of mortality risks to Neanderthal adaptation are rarely considered, it is clear that in other species reliant on hunting mortality risks are highly significant and drive biological and behavioural adaptations. Mortality risks from injury typically play a significant role in prey choice of predators in general (Mukherjee and Heithaus, 2013). African wild dogs can be killed or severely injured by the herbivores which they hunt for example (Creel and Creel, 2002). Predators such as lions are not only less efficient foragers when injured but also can be killed by their competitors (Mukherjee and Heithaus, 2013). Severe injuries bring a high risk of mortality, and predators will avoid not only dangerous prey, but habitats which are dangerous, either because of the risks of being killed by other predators or because of the risk of injury in moving through complex terrain. Few predators prey on ibex for example as they reduce their predation risks by occupying steep shelves and rugged habitats in which predators run a notable risk of injury (Kotler et al., 1994). Wolves often avoid dangerous prey, particularly if lacking older animals with necessary knowledge and skills to avoid injury (MacNulty, 2002; Stahler et al., 2006), and wolf packs that have lost older members tend to no longer be able to hunt dangerous prey such as bison or moose (Dutcher and Dutcher, 2018; Sand et al., 2006). Perhaps most significantly it is in those packs which hunt dangerous prey, and rely on accumulated knowledge, that wolves are most likely to

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Table 2
The effects of environment and adaptation on pressures to reduce mortality risk from injury in Neanderthals.

Environmental pressures on reducing mortality risk from injury	Neanderthal adaptations increasing selective pressures to reduce mortality risk from injuryv
North temperate environments >	*Demography >*
• Increased mortality risk from cold including risk to vulnerable infants • Increased injury and mortality risks from high mobility in cold environments • Injury risks from hunting large mammals • Stress related injuries from endurance activities • Risky, seasonal and unreliable resources, placing pressures on hunting success (few second chances) and on ensuring sustained resources for pregnancy, lactation and young infants	• Small group sizes imply increased interdependence (the loss of one individual has a greater effect within a smaller group) • High degree of relatedness within groups favours greater investments in the wellbeing of others. • High degree of relatedness increases risk of certain genetic diseases and conditions
Contemporary environments in Western Eurasia >	*Resource exploitation >*
• Low plant biomass and higher animal biomass leading to dependence on hunting (placing hunters under risk of injury) • Megafaunal herbivores (such as bison, mammoth and woolly rhinoceros) are more dangerous than smaller animals • Exceptionally large carnivores (such as sabre cats) increase injury risk from competition and from predator attacks	• Close encounter hunting increases risk of injury through direct engagement with prey • Reliance on skilled hunting implies that hunting efficiency increases with age, increasing relative payoffs for survival of older members of the group • Vulnerability of offspring to cold and predation increases reliance on infant care skills and knowledge of older group members

compensate for mortality risk through injury by caring for and provisioning the injured (Barber-Meyer et al., 2016). In comparison hominins are more naturally vulnerable to injury than carnivores, faced more significant adaptive pressures to improve the survival of their own injured group members and moreover had a far greater cognitive capacity to find the means to reduce mortality risks.

5. The implications of healthcare provisioning as an adaptive response to mortality risks

A strategy of mitigating injury and mortality risk through healthcare provisioning would explain several previously enigmatic elements of Neanderthal behaviour.

Most obviously healthcare provisioning explains how Neanderthals were able to occupy a predatory niche in competition with large carnivores from which the risk of mortality from injury would otherwise have precluded them. Neanderthal's ‘punch above their weight’ as a predator and they tackle far larger game than ecological models would suggest should be possible for example (Dusseldorp, 2012). Moreover recorded injury rates in other predators are significantly lower and injuries typically less severe than those seen in Neanderthals. Injury rates in birds of prey (such as broken toes, talons, flight feathers and injured eyes) vary between around 6–19%, whilst around 5–10% of large cats have fractured canines (see Mukherjee and Heithaus, 2013). In contrast almost all Neanderthals seem to have suffered at least one severe injury, with many suffering several instances of injury or illness. It even seems to have been rare to reach adulthood without a significant injury (Trinkaus and Zimmerman, 1982; Berger and Trinkaus, 1995; Pettitt, 2000). Nakahashi estimates that the rate of individuals suffering serious traumatic injury before death may have been as high as 80–95% of the population (Nakahashi, 2017). Since injury rates for other predators are limited by a lack of actualistic studies of injuries occurring in wild populations, and the estimates for Neanderthal injury are based on a skeletal publication record that may include selection biases (Estabrook, 2009), and selective mortuary practices (Spikins et al., 2014), we may be cautious about using specific estimates. Nonetheless Neanderthals appear to have used healthcare provisioning to sustain an injury rate which appears *unusually high* within a broader evolutionary context.

By surviving *after injury* Neanderthals will have accumulated their characteristic pattern of several episodes of severe injury on a scale which is not recorded in either other predators or in other primates. It can be difficult to make direct comparisons between Middle Palaeolithic and modern contexts (Estabrook, 2009), however modern humans whose environments also impose high rates of injuries and who provide healthcare similarly reflect this pattern albeit on a less extreme scale. Lessa for example notes that 27% of coastal hunter-gather-fishers in pre-colonial contexts in Brazil showed evidence of severe fractures which had healed, most commonly caused by falls in difficult coastal terrain, and 11.5% had multiple instances of fractures (Lessa, 2011). Surviving injuries from which they might otherwise have died has far reaching effects. Such survival for example extends the age profile of modern hunter-gatherers, and preserved knowledge over time, allowing a third generation to have an influence on the communication of culture (Hill et al., 2007) and may have had similarly notable effects on Neanderthals.

Neanderthal's ability to take on more risk than any similar predator may even explain their apparently daring (or blasé) attitudes to tackling prime adults at various sites (White et al., 2016), whilst other predators by necessity would focus on the weak and vulnerable.

6. The wider evolutionary significance of healthcare provisioning

Healthcare provisioning affects the ecology and evolution of hominins, as perhaps seen most clearly in Neanderthals. It might be tempting to further conclude that these archaic humans further displayed some kind of cognitive adaptation to a high risk, high injury niche. Genes regulating dopamine production, and influencing patterns of risk taking, have been influenced by patterns of Palaeolithic migration (Chen et al., 1999; Matthews and Butler, 2011) and even historical subsistence practices (Kidd et al., 2014) for example. However a broader perspective on pro-social behaviour would instead suggest that pro-sociality has been integral to human adaptation from much earlier periods, with substantial behavioural plasticity of pro-social behaviour according to context being part of that adaptation (House et al., 2013; Rajhans et al., 2016). In modern contexts high risk environments increase propensities to altruism through normal behavioural plasticity according to context (Li et al., 2013) as does dependance on collaborative hunting of very large and dangerous game (eg whale hunting, (Heinrich et al., 2004). In cognitive terms, Neanderthal's willingness to care for injured and ill group members most likely reflects simply that they were humans coping with the particular challenges that their lifestyles entailed.

The longer evolutionary history of healthcare provisioning is nonetheless likely to have influenced the path of human evolution in various different ways (Bastir, 2018). Healthcare can have a direct effect, such as in the relationship between foetal brain size and

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pelvis shape in Neanderthals, implying a characteristic half turn of a foetus at birth which is unlikely to have evolved without assisted births (León et al., 2008). However even provision of moderate care can influence the selective advantages and disadvantages of genes linked to several traits, such as local adaptation of the TRPM8 cold receptor gene with increasing latitude, which whilst protecting from effects of cold is also associated with migraine susceptibility (Key et al., 2018). Care can also have subtle and complex effects of selection pressures, such as pressures to be pro-social and affiliative (Hare, 2017), or to express subtle indicators of friendliness and vulnerability (Godinho et al., 2018). Positive selection for autism genes may also imply a level of social support for those who bring additional skills but may need more support (Spikins et al., 2016; Polimanti and Gelernter, 2017). Healthcare provisioning is likely to have affected many realms, from anatomy to physiology to cognition and further research might help us to understand these wider evolutionary implications of healthcare provisioning both in Neanderthal populations and beyond.

7. Conclusions

Care for ill and injured group members is likely to have been part of hominin adaptation since at least the emergence of the genus Homo. Like food sharing, collaborative defence, collaborative hunting and collaborative parenting, healthcare provisioning will have functioned to mitigate risks in highly collaborative and interdependent groups.

For Neanderthals healthcare provisioning may have been essential to survival. They will have faced unique ecological challenges, not only directly from risky and unreliable environments but also from the injury risks imposed by the need to exploit large and dangerous game animals in competition with exceptionally large predators. Particularly high pressures will have been placed on the means to reduce mortality risk, including through healthcare provisioning. Added to which Neanderthal adaptations, including high energy requirements, small closely related groups, and a dependence on skills and knowledge to exploit resources, will also have elevated the risks from loss of any group members and the relative benefits of healthcare provisioning. Visible cases of 'costly' care in the archaeological record are likely to be the tip of the iceberg of far more common cases of more minor injuries requiring care and provisioning to ensure survival.

Few would question that Neanderthal occupation of much of Western Eurasia was reliant on hunting technology, shelter, fire or clothing, nor that these populations relied on knowledge, skill and technological understanding to acquire the large herbivores which made up much of their diet in most of the regions occupied. However the implications of reducing mortality risks through healthcare provisioning has yet to be seen in adaptive terms, even though Neanderthals will have experienced notable selective pressures to reduce mortality risk from several causes. Pressures from predation and hunting in difficult terrain will also have led to risks of injury and mortality in even the most favourable environments. However in cooler and more arid environments in particular pressures on abilities to buffer injury risks through whatever means, including through healthcare provisioning, will have been the most intense.

Caring for ill and injured group members is part of being human. However such healthcare may have been particularly key to making the injury risks imposed by high mobility, hunting of large game, and engagements with predators within small groups of robustly built and closely related archaic humans sustainable. We argue that healthcare provisioning is a previously unrecognised and significant adaptation which improved survival in hominins in general, influenced human evolution in other realms, and was particularly significant to the viability of Neanderthal occupation.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quascirev.2018.08.011.

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